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Author(s): Robert N. Reed, Brian D. Todd, Oliver J. Miano, Mark Canfield, Robert N. Fisher, and Louanne McMartin
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Ecology and Control of an Introduced Population of Southern Watersnakes (*Nerodia fasciata*) in Southern California

Robert N. Reed[1,5], Brian D. Todd[2], Oliver J. Miano[2], Mark Canfield[3], Robert N. Fisher[4], and Louanne McMartin[3]

[1] U.S. Geological Survey, Fort Collins Science Center, 2150 Centre Avenue, Building C, Fort Collins, CO 80526, USA
[2] Department of Wildlife, Fish and Conservation Biology, University of California, Davis, One Shields Avenue, Davis, CA 95616, USA
[3] U.S. Fish and Wildlife Service, Pacific Southwest Region, 850 S. Guild Avenue, Suite 105, Lodi, CA 95240, USA
[4] U.S. Geological Survey, 4165 Spruance Road Suite 200, San Diego, CA 92101-0812, USA

Abstract: Native to the southeastern United States, Southern Watersnakes (*Nerodia fasciata*) are known from two sites in California, but their ecological impacts are poorly understood. We investigated the ecology of Southern Watersnakes in Machado Lake, Harbor City, Los Angeles County, California, including an assessment of control opportunities. We captured 306 watersnakes as a result of aquatic trapping and hand captures. We captured snakes of all sizes (162–1063 mm snout–vent length [SVL], 3.5–873.3 g), demonstrating the existence of a well-established population. The smallest reproductive female was 490 mm SVL and females contained 12–46 postovulatory embryos (mean = 21). Small watersnakes largely consumed introduced Western Mosquitofish (*Gambusia affinis*), while larger snakes specialized on larval and metamorph American Bullfrogs (*Lithobates catesbeianus*) and Green Sunfish (*Lepomis cyanellus*). Overall capture per unit effort (CPUE) in traps declined with time during an intensive 76-d trapping bout, but CPUE trends varied considerably among traplines and it is unlikely that the overall decline in CPUE represented a major decrease in the snake population size. Although we found no direct evidence that Southern Watersnakes are affecting native species in Machado Lake, this population may serve as a source for intentional or unintentional transportation of watersnakes to bodies of water containing imperiled native prey species or potential competitors.

Key words: Diet; Fat body mass; Invasive species; Los Angeles; Reproduction; Trap success

When most herpetologists think of invasive snakes, Brown Treesnakes (*Boiga irregularis*) and Burmese Pythons (*Python molurus bivittatus* or *P. bivittatus*) are likely to come to mind. The former has eliminated most birds from the island of Guam since its accidental introduction about 50 yr ago (Savidge 1987), whereas the latter is a more recent introduction to southern Florida, USA, and appears to have caused major reductions in native mammal populations (Dorcas et al. 2012; McCleery et al. 2015). As snakes go, these two species are dissimilar in ecology and in the ecosystems into which they were introduced, but they are similarly notable in terms of their impacts and in that they have garnered extensive media attention. Several other species of snakes have established nonnative populations around the globe, however, and the number of known introductions of exotic snakes has increased exponentially in recent decades (Kraus 2009). The frequency and taxonomic diversity of introductions suggest a future in which additional populations of introduced snakes will become established.

The introduction of watersnakes of the genus *Nerodia* into parts of western North America has generated interest in them as potentially invasive species (Rose et al. 2013). The genus includes 10 semiaquatic species in North America with native distributions east of the Rocky Mountains (Ernst and Ernst 2003). They feed on a wide array of aquatic vertebrates, particularly fish and frogs (Mount 1975; Ernst and Ernst 2003; Gibbons and Dorcas 2004). In western North America, many freshwater fishes and amphibians are in decline and are protected as threatened and endangered species, or are of conservation concern (Fisher and Shaffer 1996; Moyle et al. 2011). This has generated concern about possible impacts of nonnative watersnakes on native species that might serve as prey (Miano et al. 2012). Additionally, west of the Rocky Mountains, gartersnakes (genus *Thamnophis*) have radiated to reach their peak diversity and occupy many of the semiaquatic niches occupied by watersnakes in eastern North America (Rossman et al. 1996). Several species of *Thamnophis* are listed on federal or state endangered species lists or are otherwise considered species of conservation concern. A recent study found that large parts of western North America have suitable climate and habitat capable of supporting nonnative populations of Common Watersnakes (*N. sipedon*) and Southern Watersnakes (*N. fasciata*), and identified several species of fish, amphibians, and gartersnakes that could be at risk from nonnative watersnakes (Rose and Todd 2014). For these reasons, it is important to understand the distribution, ecology, and potential for controlling exotic populations of nonnative watersnakes.

Southern Watersnakes are native to the southeastern United States, where they are distributed along the Coastal Plain from North Carolina to eastern Texas and throughout Florida (Gibbons and Dorcas 2004). Among at least four introductions of three species of *Nerodia* to the State of California (Balfour and Stitt 2008; Rose et al. 2013) are two populations of *N. fasciata*. One population has been known from the vicinity of Folsom, near Sacramento, for >20 yr (Balfour and Stitt 2002; Stitt et al. 2005; Balfour et al. 2007). The second was first reported in 2006 from Machado Lake in Ken Malloy Harbor Regional Park, Harbor City, California, in the southwestern part of greater Los Angeles (Fuller and Trevett 2006). The population status of the Harbor City population is largely unknown. The purpose of our study was to assess the status and ecology of the Harbor City population, evaluate the feasibility of eradication, and gain a better understanding of the potential impacts of these exotic snakes in an urban habitat.

Materials and Methods

Study Site

Machado Lake is a shallow impoundment of ~16-ha surface area in Ken Malloy Harbor Regional Park (97 ha

[5] Correspondence: e-mail, reedr@usgs.gov

Fig. 1.—Aerial photo of Machado Lake and surrounding areas, Harbor City, California, USA (inset). Ephemeral wetlands mentioned in text are located south and southwest of the baseball diamond visible in the photo area. A color version of this figure is available online.

including the lake; Fig. 1). The lake receives runoff and stormwater from a 6300-ha urban drainage via the channelized Wilmington Drain (formerly the Bixby Slough), as well as from several stormwater drains. As a result, the lake is considered impaired by bacteria, ammonia, copper, and lead (City of Los Angeles 2014). Depending on the season and intensity of recent vegetation-control efforts, as much as a third of the lake can be densely covered in exotic Water Primrose (*Ludwigia* sp.). Native Tule Bulrush (*Scirpus* spp.) and exotic Cattail (*Typha* spp.) are also common along the margins of the lake. Although heavily polluted, the park harbors remnants of native riparian forest and freshwater marsh that have largely been eliminated from the rest of Los Angeles County. As a recipient of urban runoff and lacking any surface flow outlet to the nearby Port of Los Angeles, Machado Lake is generally isolated from other water bodies. This reduces the odds that individual watersnakes will disperse without human intervention to other areas with higher numbers of native species that would serve as prey, including species of conservation concern. Among nearby aquatic systems, the heavily channelized and intermittent Dominguez Channel (5.5 km away) and Los Angeles River (8.2 km away) lie to the east; to the west, extensive hills separate Machado Lake from the Agua Amarga reserve (10 km away).

Capture Methods

We trapped snakes in Machado Lake using a mix of plastic (Model 700, Gator Buckets) and metal (Gee's minnow trap, Tackle Factory) traps. We widened the openings of the metal traps from 2.5-cm to 3.0–3.5-cm diameter, because this promotes higher capture rates of large-bodied snakes (Willson et al. 2008). We set traps such that the entire funnel apex was submerged, but the top of the trap was above water to allow captured animals access to air. The traps were self-baiting with Western Mosquitofish (*Gambusia affinis*) and other potential prey items (Winne 2005). Depending on density of aquatic vegetation, traps were either placed directly in floating vegetation or were attached to bamboo stakes to prevent them from sinking. Traps were placed in linear or sinuous arrays through or on the edge of aquatic vegetation (primarily *Ludwigia*) in water depths of 0.25–1.5 m, and were checked daily by biologists on foot or in a kayak. To assess whether drift fences increased capture rate, we erected three drift-fence arrays in Summer 2010 using plastic erosion-control fabric equipped with stakes, ensuring that ≥20 cm of the fence was out of the water and ≥30 cm was submerged. Each fence was 8 m long, with 2 plastic and 2 metal traps on each side (8 traps per fence). As controls for the fences, we placed an equivalent number and composition of traps 10 m from the fence in similar microhabitat and water depth. We also conducted a limited amount of nocturnal visual searching on foot in shallow areas of the lake, using headlamps to locate snakes and capturing them by hand. Because management agencies requested that all captured snakes be removed, we were not able to conduct mark–recapture analysis to obtain a rigorous estimate of population size. Sampling occurred on multiple occasions over 2 yr, as follows: 22–30 September 2009 (920 trap-nights), 30 April–7 May 2010 (1099 trap-nights), and 6 July–19 September 2010 (13,335 trap-nights). We conducted 150 trap-nights of sampling in the Wilmington Drain, as well as limited sampling in two shallow and intermittent ponds ~500 m southeast of Lake Machado (150 trap-nights, 5 person-hours of visual surveys; these ponds can be seen south of the baseball diamond in Fig. 1).

All snakes were euthanized with an overdose of inhalant Isoflurane within 24 h of capture. Snakes captured in 2009 were necropsied immediately after euthanasia, whereas those captured in 2010 were necropsied after having been frozen for 5–8 mo. We weighed and measured all snakes during necropsy, examined gastrointestinal tracts for prey items, and recorded evidence of previous injuries (scars, etc.). Snakes captured during May–September of 2010 were subjected to more intensive necropsy, including removing and weighing fat bodies, counting the number of follicles or embryos in females, and measuring the largest and smallest follicles in females.

We used chi-square tests to assess goodness of fit between observed and expected values. We used the Shapiro–Wilk test to assess normality of distributions. When assumptions of linear models were met, we used unpaired two-tailed *t*-tests to examine whether means of two groups were statistically different from one another. When assumptions of linear models were not met, we used the Kruskal–Wallis nonparametric equivalent of one-way analysis of variance to test for difference between two or more groups of response variables. We used linear regression to examine the effect of time on both capture per unit effort (CPUE; traps only) and volume of the largest follicle in reproductive females, and Pearson product-moment correlation analysis to examine relationships between fat body mass and body length. Descriptive statistics and analyses were calculated in SYSTAT v13 (Systat Software, Inc.) and Microsoft Excel (Microsoft Corporation). We set $\alpha = 0.05$ for all statistical analyses; values are presented as means ±1 SD.

Results

Body Size and Capture Rate

We captured 306 Southern Watersnakes, including 47 in September 2009, 62 in May 2010, and 197 during July–October 2010, consisting of 275 trap captures and 31 hand captures. Of these 306 individuals, 303 were from Machado Lake and 3 were from the Wilmington Drain. We received an additional 5 snakes trapped between 26 September and 1 October 2010 in Wilmington Drain from a collaborator. We detected no snakes in the ephemeral ponds to the southeast of Machado Lake by either traps or visual surveys. The mean snout–vent length (SVL) of snakes captured in plastic traps was 461 ± 145 mm (range = 168–980 mm), slightly smaller than the mean size of snakes captured in metal traps (481 ± 148 mm, range = 224–880 mm). Snakes captured during visual surveys averaged 437 ± 207 mm (range = 162–1023 mm). There was no difference in SVL as a function of capture method (Kruskal–Wallis $H = 2.04$, df = 2, $P = 0.36$). Drift fences did not increase snake capture rates because we captured 30 snakes using traps along drift fences and 21 in the adjacent control traps ($\chi^2 = 1.59$, df = 1, $P = 0.21$). Among all snakes, 4.6% exhibited scars or other signs of previous injury. Not all variables could be recorded for every snake; therefore, sample sizes vary in results given below.

During the intensive trapping effort in 2010, we deployed 12 trap arrays in Machado Lake for various lengths of time. Overall CPUE during this period was 0.019 snakes per trap-night, and ranged from 0.009 to 0.062 across the 12 arrays. CPUE declined during the course of the trapping effort when calculated as the effect of trapping week on overall mean CPUE across trap arrays (linear regression, $r^2 = 0.77$, $m = -0.003$, $b = 0.046$, $P < 0.01$).

Size and Sex

Among all captured snakes, body size averaged 456 mm in SVL and 130 g in mass. Females attained larger body sizes than did males (Table 1; Fig. 2), although only mass was statistically different when considering animals of all size classes (SVL, $t = 0.85$, df = 236, $P = 0.40$; mass, $t = 4.03$, df = 236, $P < 0.001$). Among individuals >500 mm in SVL (reproductively mature), however, females were longer ($t = 3.59$, df = 124, $P < 0.001$), and the largest female was more than twice the mass of the largest male. The six smallest individuals, presumably recent neonates, averaged 170.7 mm in SVL and 4.1 g in mass (ranges = 162–185 mm and 3.5–4.8 g, respectively). Relative tail length (tail length divided by total length) was greater in males than in females (0.27 vs. 0.24, respectively; $t = -13.78$, df = 186, $P < 0.001$; Table 1). We captured more females (187) than males (119) for a ratio of 1.57:1 that differed from 1:1 ($\chi^2 = 15.1$, df = 1, $P < 0.001$). We were unable to quantify variation in capture probability by sex (e.g., Tyrrell et al. 2009) and also funnel traps have known size biases in capture probabilities (Willson et al. 2005, 2008); therefore, this ratio is not necessarily representative of the overall population.

TABLE 1.—Summary statistics of body sizes of Southern Watersnakes (*Nerodia fasciata*) captured from Machado Lake, Harbor City, California, USA. Tail lengths were omitted from analysis for 58 individuals (28 females, 30 males) with stub tails. Means are reported ±1 SD. Sample sizes are reported after ranges, and vary because not all variables were recorded for all individuals.

	Mass (g)		Snout–vent length (mm)		Tail length (mm)	
	Mean	Range	Mean	Range	Mean	Range
Overall	130.0 ± 137.6	3.5–873.3 (n = 306)	456.1 ± 150.3	162–1023 (n = 306)	147.4 ± 43.5	58–254 (n = 248)
Females	149.2 ± 163.3	4–873.3 (n = 187)	463.7 ± 165.8	170–1023 (n = 187)	144.0 ± 45.9	58–254 (n = 159)
Males	100.7 ± 74.4	3.5–390.7 (n = 119)	444.2 ± 121.6	162–747 (n = 119)	153.4 ± 38.5	65–232 (n = 89)

Reproduction

Reproductive data were collected from female snakes captured during the July–September 2010 trapping bout. Among females >490 cm in SVL captured in July (n = 33), when embryos should be most apparent during necropsy, 42% contained embryos. The smallest female with embryos was 490 mm in SVL and 128 g in mass, while the largest was 766 mm and 675 g. Among 90 females >490 mm in SVL, 28 (31%) contained developing embryos while another 31 (34%) contained visible follicles. Mean litter size was 21.16 ± 1.75 (range = 12–46) among 26 females in which the number of embryos could be counted. During Summer 2010, volume of the largest postovulatory embryo increased over time (females with measured embryos captured 3 May through 1 September; linear regression r^2 = 0.20, b = −15, m = 0.41, P = 0.03). The smallest juvenile snakes (< 250 mm in SVL, n = 31) were generally captured in August and September regardless of sampling year.

Fat body mass was positively correlated with SVL (Pearson product-moment correlation, r = 0.76; Fig. 3) across all snakes. Over the course of the 2010 summer sampling season, female snakes of reproductive size (>490 mm SVL; n = 63) exhibited a weak positive correlation between relative fat body mass (fat mass divided by total mass) and date of capture (r = 0.12), with a wide range of fat body masses late in the sampling period. Using the same size cut-off for males (n = 27) yielded a weaker relationship between these variables (r = 0.05) over the course of the sampling period.

Diet

Prey identified from snakes captured during visual surveys included Western Mosquitofish, Green Sunfish (*Lepomis cyanellus*), and a single Brown Bullhead (*Ameiurus nebulosus*); 29% of hand-captured individuals contained prey. Prey identified from snakes captured in traps included *G. affinis, L. cyanellus,* and tadpoles and small metamorphs of American Bullfrogs (*Lithobates catesbeianus*). Snakes <400 mm in SVL contained only *G. affinis*, except for one snake (SVL = 393 mm) that had consumed a bullfrog tadpole; 33% of these small snakes contained identifiable prey. Among snakes >400 mm in SVL, *L. catesbeianus* was more prevalent among gut contents (51.4% of identifiable prey) and *G. affinis* became less prevalent (not observed among snakes > 580 mm). Among the 10 largest snakes (720–1023 mm in SVL), identifiable prey included *L. catesbeianus* (n = 5), *Lepomis cyanellus* (n = 4), and the bullhead. Overall, 32% of trapped snakes contained identifiable prey (Table 2).

DISCUSSION

Our results support the conclusion that Machado Lake is home to a large population of Southern Watersnakes, including all size classes and many reproductive individuals. We do not know how long Southern Watersnakes have been established in Machado Lake. A single individual was reported from "a pond in west Los Angeles" in 1976 (Bury and Luckenbach 1976:8), but Fuller and Trevett (2006) presented evidence that this observation might have been from a different park in Long Beach. The pet trade is suspected as being the most likely introduction pathway for the Machado Lake population because Southern Watersnakes have long been listed on wildlife dealers' price lists and because it seems relatively unlikely that an aquatic snake from the southeast United States would be unintentionally transported to a lake in southern California via cargo, aquaculture, or by other means. Snakes of the genus *Nerodia*

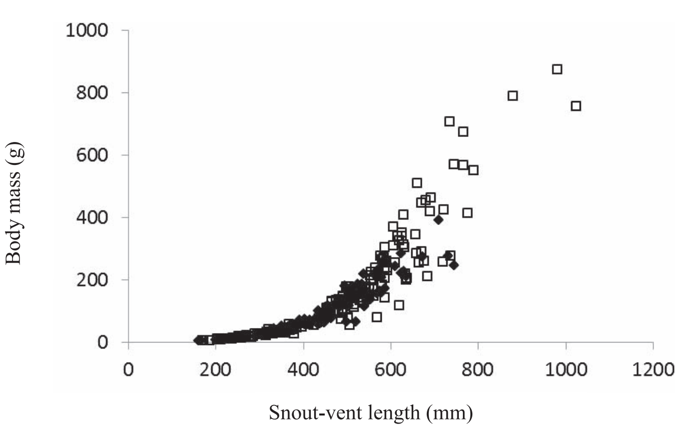

FIG. 2.—Scatterplot of mass as a function of snout–vent length for female (open squares) and male (filled diamonds) *Nerodia fasciata* removed from Machado Lake, Harbor City, California, USA.

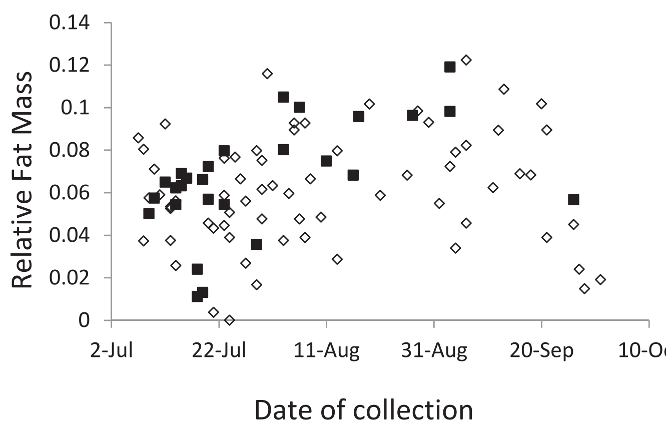

FIG. 3.—Scatterplot of relative fat mass (fat body mass divided by total body mass) as a function of collection date for adult female (open diamonds, n = 63) and male (filled squares, n = 27) *Nerodia fasciata* (>490 mm SVL) removed from Machado Lake, Harbor City, California, USA, during the 2010 sampling period.

Table 2.—Summary of diet of four size classes of *Nerodia fasciata* captured in Machado Lake, Harbor City, California, USA, as evidenced by prey removed from snake digestive tracts. We categorized "postlarval" *Lithobates catesbeianus* as any individual with well-developed forelimbs, regardless of the presence of a tail. See text for caveats about potential bias introduced by including snakes removed from self-baiting traps.

Diet	Snout–vent length (mm)			
	≤250	251–500	501–750	≥751
Total *n*	31	149	119	7
Number (%) containing prey	7 (23%)	52 (35%)	51 (43%)	7 (100%)
Prey species				
Gambusia affinis	7	34	5	0
Ameiurus nebulosus	0	0	0	1
Lithobates catesbeianus (larval)	0	2	4	0
L. catesbeianus (postlarval)	0	8	20	3

have been regulated as a restricted species by the California Department of Fish and Game since 2008, and importation, transportation, possession, and sale are now prohibited without a special permit. All four introductions of *Nerodia* into California are known to have occurred prior to this restriction being implemented.

One of our goals was to assess whether trapping and hand captures would appreciably reduce the overall population of Southern Watersnakes in Machado Lake. Overall, 90% of our sample was captured in aquatic traps. Nocturnal visual surveys were relatively successful (~1 snake captured per search hour), but we curtailed visual surveys after 30 person-hours for safety reasons at the suggestion of local law enforcement personnel. Although traps along drift fences captured ~50% more snakes per trap-night than did the adjacent unfenced arrays, the sample size of captures was too small for robust conclusions and the fences required regular maintenance, especially after windy days and water-level changes. The reluctance of local management agencies to allow release of any captured snakes meant that we were unable to assess efficacy of control efforts via mark–recapture, forcing us to rely on CPUE as an index of changes in population density. We observed an overall decline in mean CPUE over time during the Summer 2010 intensive trapping effort, and it is tempting to infer that our efforts were effective in reducing overall snake densities in Machado Lake. If this were the case, we would expect CPUE of each array to mirror the overall trend, but our results did not support this prediction. Intensive snake trapping (86 traps/ha) in an isolated wetland in South Carolina yielded a minimum density of 76 Southern Watersnakes per ha (Willson et al. 2011); the density of introduced Common Watersnakes in a northern California wetland was estimated at 56/ha (Rose et al. 2013). In contrast, over 76 d in 2010, we removed only 12 snakes/ha in a 16-ha lake with a trapping intensity that never exceeded 11 traps/ha. Combined with low initial probabilities (0.02–0.05) of trap capture for Southern Watersnakes in South Carolina (Willson et al. 2011), and the fact that about one-third of trapped Southern Watersnakes escape from traps (Willson et al. 2005), these comparative results suggest that our sample of snakes from Machado Lake represented a small proportion of the total population size.

Our discussion of the body sizes and sex ratio of captured snakes must be prefaced by acknowledging that both trap and hand captures are almost certainly biased by varying detection probabilities among size classes, ages, and sexes. These biases are widespread among snake studies (e.g., Tyrrell et al. 2009), and are established for watersnakes including *N. fasciata* (Willson et al. 2008, 2011). Such caveats about detection probabilities also apply to most of the historical literature with which we can compare our results (although this bias was largely unappreciated in historical literature), reducing our confidence in the strength of comparisons. Overall, our results were not highly divergent from those found for populations in the native range. Presumptive neonates at Machado Lake averaged 170 cm in SVL and 4 g in body mass, similar to sizes of captive-born Southern Watersnakes reported by Scudder-Davis and Burghardt (1996). Means of both mass and SVL were lower in the Machado population compared with a native population in South Carolina (SC; female mass = 149 g in Machado vs. 246 g in SC; male mass = 100 g in Machado vs. 113 g in SC; female SVL = 456 mm in Machado vs. 638 mm in SC; male SVL = 444 mm in Machado vs. 535 mm in SC; Semlitsch and Gibbons 1982). The South Carolina study included no recent neonates, however, thus skewing means toward larger sizes. The maximum values for snakes from the Machado population were larger than the maxima for those from South Carolina for all but female mass: 873 g (Machado) vs. 990 g (SC). Our smallest pregnant female was 490 mm in SVL, smaller than the minimum size of 550 mm reported from the native range in Louisiana (Kofron 1979).

The largest female in our data set (captured by hand) was longer than any of the Southern Watersnakes captured during multiple years of sampling in South Carolina (J.D. Willson, personal communication); on several occasions, we observed even larger and apparently gravid females basking on floating debris in Machado Lake. These snakes were larger than any snake captured in minnow traps, emphasizing the size-specific variability in trap-capture rates across sizes and sexes, and implying that our estimates of reproductive capacity might have been considerably higher if these animals had been included in our necropsy data set. If the largest gravid females are aphagic and sedentary during late gestation, then neither intercept (i.e., drift fences with traps) nor attractant (self-baiting with prey) traps are likely to be effective. Removing available surface debris in the lake and replacing it with basking traps (Vogt 2012) especially designed to capture and retain snakes might be a more effective means of removing this demographically important segment of the snake population.

Small, postovulatory embryos were detected in four females captured during May 2010, implying that vitellogenesis likely occurred in spring. Embryo sizes increased markedly among snakes captured in July and August, and the smallest snakes were found in August and September, indicating that parturition occurred during this period. These patterns are similar to vitellogenesis and parturition dates in the native range (Kofron 1979; Lorenz et al. 2011). Among females >490 cm in SVL captured in July (n = 33), when embryos should be most apparent during necropsy, 42% contained embryos. Furthermore, our observation that female fat body mass exhibited wide variation starting in early September also indicates that parturition occurred during this period, but that not all adult females in the population had reproduced. Female reproduction might therefore be less frequent than once per year (possibly biennial) at Machado Lake. In a study of another invasive population of Southern Watersnakes near Folsom, California, 85% of captured adult females were gravid (Stitt et al. 2005). It is not possible to discern whether the Folsom population has high reproductive success or whether basking pregnant females are particularly vulnerable to hand capture (the method that yielded the most snakes in that study). Our observed mean litter size (21; based on number of oviductal embryos) is similar to mean values reported for both native (Semlitsch and Gibbons 1982; Palmer and Braswell 1995; Ernst and Ernst 2003) and introduced (Stitt et al. 2005) populations, and our observed maximum of 46 embryos underscores the potential for new extralimital populations to be established based on introduction of even a single, large, pregnant female of this species.

Southern Watersnakes are known to be generalist feeders, with >40 prey taxa reported in the literature (Ernst and Ernst 2003; Gibbons and Dorcas 2004). Our necropsies revealed only four prey species consumed, predominantly *G. affinis* and *Lithobates catesbeianus*, with lower prevalence of sunfish. These results are similar to those reported for Southern Watersnakes from Louisiana by Mushinsky et al. (1982), who noted an ontogenetic dietary shift in which small snakes eat fish (primarily *G. affinis*), whereas larger individuals switch to frogs and larger fish species (including sunfish and catfish). Dietary data from snakes captured in traps are probably biased because of the occasionally high densities of prey species that accumulate in traps over the course of a day. We sometimes captured dozens of bullfrog tadpoles and hundreds of mosquitofish in a single trap, and we recorded up to 17 mosquitofish inside trapped snakes but not more than two in hand-captured snakes. Therefore, although our results might have captured the species composition of the snake diet, the number of individual prey items in a snake was biased by the method of capture.

We did not capture or observe any fish, frogs, or snakes native to California during our snake trapping efforts, visual surveys, or day-to-day tasks at Machado Lake, nor did we find any native species inside watersnakes during necropsies. Instead, we encountered a wide range of introduced aquatic fauna in the lake and in snake stomach contents, making it difficult to assess the potential ecological impacts of this exotic watersnake population. It is unsurprising that a snake native to the southeastern United States was able to become established in a lake already occupied by many prey species introduced from its native range. Machado Lake could be considered primed for additional invasions by species from the southeastern United States.

Given a lack of observed impacts to native species, the isolated nature of the lake, and no quantified societal or economic costs, Southern Watersnakes in Machado Lake could perhaps be considered exotic, but not invasive. Such an interpretation could be used to downplay the risks associated with this population. This would be short-sighted, however, because snakes in Machado Lake represent a source population from which individuals could be intentionally transported (cf. Edwards et al. 2014) to areas that are more ecologically sensitive. The habitat and dietary generalism, and reproductive capacity, of *N. fasciata* imply high risks of population establishment and impacts should individuals be translocated to water bodies in California that do contain imperiled native species. Major ecological restoration of Machado Lake and the Wilmington Drain is currently underway (City of Los Angeles 2014), and these activities might be beneficial to Southern Watersnakes by increasing prey abundances and providing opportunities for unintentional transport of snakes to other water bodies via construction equipment or other pathways. Moreover, the lake is likely to receive even more exotic species in the future; on three occasions we observed brightly colored aquarium gravel in shallow water along the shore, indicating spots where captive aquatic organisms had been recently released. Our field assistants also observed a group of monks releasing large numbers (estimated in the thousands of individuals) of small goldfish and koi as part of a religious ritual. For generalist predators such as Southern Watersnakes, adding potential prey species is likely to provide even greater opportunities to attain high densities in the lake, thereby increasing the likelihood of intentional or inadvertent transport to other water bodies. Public education via informational signs in multiple languages paired with outreach to specific user groups could potentially reduce the rate of new introductions.

Draining both Machado Lake and Wilmington Drain and embarking on an intensive snake-control program would provide the best chance of eradication, but such a course of action would be opposed by park visitors, fishermen, and birdwatchers. Traps, visual surveys, and/or other available control tools might serve to suppress the population of an undrained lake, but even a sustained high-intensity effort might be insufficient to achieve complete eradication. Biological control, reproductive inhibition, and similar methods are unproven for operational control of snakes, and would require long-term research investments to bring them to initial stages of field testing (Reed and Rodda 2009). Recent discoveries regarding the attractiveness of prey-based chemical cues (parvalbumins) to Southern Watersnakes (Smargiassi et al. 2012), and/or estradiol-driven induction of female sex pheromone in male thamnophiine snakes as an attractant for other males (Parker and Mason 2012), appear worthy of exploration in a control context.

As compared with many other semiaquatic snakes, Southern Watersnakes tend to exhibit fairly high detection probabilities using minnow traps as a sampling method (Durso et al. 2011), suggesting that vigilant land managers might be able to detect incipient populations elsewhere outside the native range before high population densities are achieved. Molecular tools such as environmental DNA (Hunter et al. 2015) might provide a cost-effective tool for detecting watersnake populations at low densities. If incipient populations are detected, intensive rapid-response efforts might allow local eradication.

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